Contributed Paper

Golden Eagle fatalities and the continental-scale consequences of local wind-energy generation

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Abstract: *Renewable energy production is expanding rapidly despite mostly unknown environmental effects on wildlife and habitats. We used genetic and stable isotope data collected from Golden Eagles* (Aquila chrysaetos) *killed at the Altamont Pass Wind Resource Area (APWRA) in California in demographic models to test hypotheses about the geographic extent and demographic consequences of fatalities caused by renewable energy facilities. Geospatial analyses of δ^2H values obtained from feathers showed that ≥25% of these APWRA-killed eagles were recent immigrants to the population, most from long distances away (>100 km). Data from nuclear genes indicated this subset of immigrant eagles was genetically similar to birds identified as locals from the δ^2H data. Demographic models implied that in the face of this mortality, the apparent stability of the local Golden Eagle population was maintained by continental-scale immigration. These analyses demonstrate that ecosystem management decisions concerning the effects of local-scale renewable energy can have continental-scale consequences.*

Keywords: renewable energy, SNP, stable hydrogen isotope, wind–wildlife interactions

Fatalidades del Águila Dorada y Consecuencias a Escala Continental de la Generación Local de Energía Eólica

Resumen: *La producción de energía renovable se está expandiendo rápidamente a pesar de los muchos efectos desconocidos sobre la vida silvestre y sus hábitats. Utilizamos los datos genéticos y de isotopos estables recolectados de águilas doradas* (Aquila chrysaetos) *muertas en el Área de Recursos de Aire del Paso de Altamont (ARAPA) en California en modelos demográficos para probar las hipótesis sobre la extensión geográfica y las consecuencias demográficas de las fatalidades causadas por las instalaciones de energía renovable. Los análisis geoespaciales de los valores de δ^2H obtenidos de las plumas mostraron que ≥25 % de estas águilas muertas en ARAPA eran migrantes recientes hacia la población, la mayoría desde distancias lejanas (>100 km). Los datos de los genes nucleares indicaron que este subconjunto de águilas inmigrantes era genéticamente similar a las aves identificadas como locales a partir de los datos de δ^2H. Los modelos demográficos insinuaron que, de frente a esta mortalidad, la estabilidad aparente de la población local de águilas doradas fue mantenida por una inmigración a escala continental. Estos análisis demuestran que las decisiones de manejo del ecosistema con respecto a los efectos de la energía renovable a escala local pueden tener consecuencias a escala continental.*

Introduction

Renewable-energy development is rapidly emerging as a defining characteristic of 21st century economies and geopolitical decision making (USDoE 2015). Governments globally are promoting renewable energy development through tax credits, subsidies, and supportive environmental permitting (e.g., EWEA 2015; USDoE 2015). Consequently, growth in the renewable-energy sector has been dramatic; renewables comprise 56% of new electrical-generation capacity installed since 2000 in Europe (EWEA 2015) and >60% of new electricity-generation installations in the United States in 2013 (US-DoE 2015).

Energy generation from renewable resources often is viewed favorably because it releases relatively few greenhouse gases and its other associated environmental impacts (e.g., wildlife fatalities, road building, clearing, and habitat fragmentation) are thought to be primarily local in nature (Spellman 2014). Nevertheless, renewable energy development and production has substantial environmental consequences. In particular, an estimated 140,000 –328,000 birds (Loss et al. 2013) and 500,000 – 1.6 million bats (Arnett & Baerwald 2013; Hayes 2013) are killed by wind turbines each year in the United States. Likewise, many other species are killed or their behavior or habitats altered at renewable energy facilities worldwide (Spellman 2014; Voigt et al. 2015). Despite the large number of wildlife killed at renewable energy facilities, key questions remain about these fatalities. Critically, it is unclear whether mortality rates are sustainable for affected populations. Thus, characterizing the scope of this mortality is central to the successful implementation and management of global renewable-energy development.

Golden Eagles (*Aquila chrysaetos*) are of great conservation concern and are among the highest profile wildlife species killed at renewable-energy facilities (Hunt 2002). Golden eagles occur at low densities and are long-lived, slow-reproducing, partially migratory, apex predators with key biodiversity functions (Sergio et al. 2005; Watson 2010). The demographic and environmental consequences of Golden Eagle mortality are expected to be substantial because of the sensitivity of their populations to small changes in vital rates (Watson 2010). Populations of Golden Eagles in western North America (i.e., western Canada, United States, and Mexico) are thought to be stable or slightly declining and likely below carrying capacity (Hoffman & Smith 2003; Millsap et al. 2013). Even though high mortality rates have occurred for several decades at some wind facilities in California, the breeding population of Golden Eagles in those local

regions has not declined (Hunt 2002; Hunt & Hunt 2006). As such, local, stable breeding populations must be sustained by high birth rates and low natural death rates (i.e., fatalities due to collisions with wind turbines are compensatory and replace natural mortality in a stable population); by immigration (i.e., turbine-associated fatalities are additive, above and beyond natural mortality in a stable population); or by some combination thereof. If mortality is additive and populations are sustained by immigration, then the effects of wind-energy-associated fatalities extend far beyond the region where they occur. Such a finding would be important to environmental impact assessments that generally consider only local-scale consequences of renewable energy development.

To inform understanding of the geographic and demographic scopes of environmental consequences of wind-energy development, we tested the hypothesis that mortality of Golden Eagles at a large wind-energy facility is compensatory. We assessed the origins of birds killed by evaluating their genetic population structure with mitochondrial, microsatellite, and single-nucleotide-polymorphism (SNP) data and the geographic location where feathers were grown as inferred from values of stable hydrogen isotopes (δ^2H). We interpreted our results in the context of genetic and stable isotope data from known-origin eagles from throughout their North American range, data on the age and sex of the dead eagles, and 87 years of banding data from Golden Eagles in western North America. We used the results of these analyses within a matrix population model to broadly evaluate the implications of our findings for eagle demography and conservation.

Methods

Sample Collection

We collected samples from 67 Golden Eagles killed at the Altamont Pass Wind Resource Area (APWRA) in California from 2012 to 2014. Intact eagle carcasses were photographed and subsequently aged based on patterns of molt and feather replacement (Jollie 1947; Bloom & Clark 2001). We performed a suite of genetic and stable isotope analyses on these samples. Not all tissue types were available from every carcass, so not all analyses were performed on all eagles (see Supporting Information for details).

We collected samples from known-origin Golden Eagles from throughout North America to serve as reference materials for stable isotope ($n = 44$) and DNA analysis ($n = 27$; details in Supporting Information).

Genetic Sample Preparation and Analysis

We subjected the DNA samples to 4 distinct assays: genetic sexing, mitochondrial DNA (mtDNA) sequencing, microsatellite genotyping, and SNP genotyping.

Nine microsatellite loci (described in Martinez-Cruz et al. 2002; Busch et al. 2005; Hailer et al. 2005; Supporting Information) were used to genotype 62 individual eagles. These 9 loci were amplified in 4 distinct reactions (1 tetraplex consisting of loci Aa11, Aa15, Aa36, and IEAAAG04; 1 triplex consisting of Hal10, Hal13, and IEAAAG13; IEAAAG14; and Aa27) resolved using an Applied Biosystems 3730 sequencer. Genotypes were assigned using GeneMapper software. All loci except Aa15 and IEAAAG14 were in Hardy–Weinberg equilibrium. Fifty eagles were sexed via polymerase chain reaction and subsequent agarose gel electrophoresis with 2550F and 2718R PCR primers (Fridolfsson & Ellegren 1999). The mtDNA sequences were generated from the control region with the primers SpiCR31 and Pro (Cadahía et al. 2009). The mtDNA fragment was purified, sequenced with dideoxy chemistry, aligned, and edited (Fahey et al. 2012).

We genotyped 52 eagles at 162 SNPs with a novel Fluidigm SNP-type assay (Doyle et al. 2016). This marker panel consisted of 159 nuclear SNPs, 2 mitochondrial SNPs, and 1 sexing SNP. Results for sex identification of eagles genotyped with both methods were in perfect concordance. The 2 mitochondrial SNPs we assayed described variation present in a 695 bp portion of the mitochondrial control region. The mtDNA haplotypes inferred with SNPs were redundant with our dideoxy sequencing efforts and the sexing SNP was redundant with the PCR assay, but each complementary technique provided independent validation of the other.

To determine the number of genetic populations represented in the samples of eagles killed at APWRA, we used GenAlEx (Rousset 2008) to calculate allele frequencies and observed heterozygosities for both SNP and microsatellite data sets (Supporting Information). We subsequently used STRUCTURE (Pritchard et al. 2000; Evanno et al. 2005) and Structure Harvester (Earl & vonHoldt 2012) to determine whether APWRA eagles are part of one or more genetically distinct populations. For both nuclear SNP and microsatellite data sets, we considered values of $K = 1 – 5$ (numbers of populations), running each value 10 times with 100,000 Markov chain Monte Carlo iterations for each value. We assumed an admixture ancestry model and allowed for correlated allele frequencies. For both SNP and microsatellite data sets, we ran STRUCTURE with uniform prior probabilities and local and nonlocal designations as a prior probability. Local and nonlocal designations were determined from stable isotope analyses. We also performed a STRUCTURE analysis of 159 SNP loci that included both APWRA-killed samples and reference samples from Golden Eagles from eastern Canada and United States. For mtDNA data, we used Arlequin version 3.5 (Excoffier & Lischer 2010) to estimate haplotype and nucleotide diversity. To evaluate mtDNA genetic differentiation between putatively local and nonlocal birds, we conducted an analysis of molecular variance with GenAlEx (Rousset 2008).

Stable Isotope Origin Assignment

Samples of body feathers were analyzed for $\delta^{13}C$, $\delta^{15}N$, and $\delta^{2}H$. We used these values to assess the geographic origins of feathers obtained from eagles killed at the APWRA as follows (see Supporting Information for rationale and details). First, we characterized $\delta^{13}C$ and $\delta^{15}N$ values to assess the potential for marine inputs in diet that would make $\delta^{2}H$ values unsuitable for geolocation. Thresholds for individuals in marine-based food webs are $\delta^{13}C$ values $> -20‰$ and $\delta^{15}N$ values $>11‰$ (Chamberlain et al. 2005; Yerkes et al. 2008; Newsome et al. 2010). Second, we used the IsoMAP assignment tool (Kennedy et al. 2011; Bowen et al. 2014), which uses a Bayesian probabilistic framework, to produce likelihood-of-origin maps for each Golden Eagle. The IsoMAP assignment tool requires as input an isoscape of $\delta^{2}H$ of precipitation ($\delta^{2}H_p$); a spatially variable standard deviation associated with that isoscape; a $\delta^{2}H_p$ value (calculated from feather $\delta^{2}H$ values [$\delta^{2}H_f$] with a transfer function); and a spatially invariant standard deviation of that $\delta^{2}H_p$ value, which represents variation in the processes that link the $\delta^{2}H_p$ values to the measured $\delta^{2}H_f$ value. We used the May–August $\delta^{2}H_p$ isoscape shown in Fig. 2 (and its associated spatially variable standard deviation) to create likelihood-of-origin maps in the IsoMAP assignment tool. We used the relationship between $\delta^{2}H_f$ and May–August $\delta^{2}H_p$ values for 264 raptors of known origin in Lott and Smith (2006) to convert mean Golden Eagle $\delta^{2}H_f$ values to May–August $\delta^{2}H_p$ values for geospatial analysis with the aforementioned May–August $\delta^{2}H_p$ isoscape in the IsoMAP assignment tool (details in Supporting Information). The spatially invariant standard deviation (1σ) of $\delta^{2}H_p$ used for these assignments was set at 22‰, which is the standard deviation of residuals of $\delta^{2}H_p$ values in the equation relating $\delta^{2}H_f$ and $\delta^{2}H_p$ (Lott & Smith 2006).

We quantified the accuracy of the likelihood-of-origin maps produced by IsoMAP for the 44 reference Golden Eagles of known geographic origin by plotting isopleth contour intervals on each map (in units of 0.1 from 0.1 to 0.9) with the Geospatial Modelling Environment (http://www.spatialecology.com/gme/). Each isopleth contains all pixels up to a given probability that are predicted to contain the location of origin for an individual. For example, the 0.3 isopleth contains the largest 30% of likelihood values. For the 44 reference Golden Eagles of known geographic origin, we recorded the value of the minimum isopleth within a 150 km² area (i.e., the estimated home range of Golden Eagles in California;

Braham et al. 2015) of the known sampling location. The distribution of these minimum isopleth values was then fitted (details in Supporting Information).

Using the fitted distribution, we implemented a Monte Carlo simulation to estimate the probability that a turbine-killed eagle was of local or nonlocal origin. For birds classified as nonlocal based on a majority-rule criterion (Supporting Information), we calculated the distance between APWRA and the boundary of the nearest 0.5 isopleth as an estimate of the minimal distance from which the bird could have originated. We chose the 0.5 isopleth for these distance calculations because the known locations of all but 2 of our 44 validation birds fell within this isopleth. We also evaluated the expected accuracy assignment for eagles of unknown origins across all possible intervals of relative probability with the approach described in Vander Zanden et al. (2014).

We used a chi-squared test of independence to assess the influence of age (juvenile, subadult, and adult), month of death, and sex on the number of nonlocal birds killed at APWRA (Zar 2010). Significant differences between the expected and observed numbers indicated increased likelihood of birds of particular age, month of mortality, and sex being nonlocal. Similar tests were performed across seasons (Supporting Information).

Bird-Banding Data

To independently evaluate the performance of our isotope-based classification scheme against other mechanisms used to evaluate eagle movement and to parameterize potential dispersal distances of eagles, we evaluated 1144 band-recovery records from North American Golden Eagles collected between 1926 and 2013 and provided by the U.S. Geological Survey (USGS) Bird Banding Laboratory. We filtered records to focus exclusively on birds with either (or both) a banding or recovery event that occurred within 500 km of the APWRA. Using these data, we evaluated the average, maximum, and minimum distance eagles were recorded to move between banding and recovery events, and we recorded the state or province in which each banding and recovery event occurred.

Population Modeling

We built (in MS Excel) a deterministic, age-structured Leslie matrix model (Caswell 2001) to describe the population biology of Golden Eagles at the APWRA (Supporting Information). We parameterized this model using demographic rates estimated in the APWRA region (annual survival = 0.84 [juvenile, HY], 0.79 [subadult 2–4 years, 2Y – 4Y], and 0.909 [adult ≥5 years, A5Y]; annual productivity = 0.46 chicks/adult [Hunt 2002]). We initiated model runs with $n = 100$ birds in each of the 6 age classes (HY–A5Y) and without immigration to

APWRA. We ran the model for 100 years, well past the point where it converged on a stable age distribution. We then compared the stable-age distribution with the distribution of ages of birds killed by turbines at APWRA and adjusted the age-specific immigration rates in our model until the modeled age distribution approximated the age structure represented by the fatalities. If the age distribution from turbine-killed eagles matched the age distribution without immigration, then our results supported the hypothesis that mortality is compensatory. If the age distribution from turbine-killed eagles matched the model with immigration, then our analyses supported the hypothesis that mortality is additive.

Results

Of the 52 turbine-killed Golden Eagles from which remains were sufficient for aging, one was <9 months old at time of death (HY), 16 were 9–20 months old (2Y), 17 were 21–32 months old (3Y), 2 were 33–44 months old (4Y), and 16 were ≥45 months old (≥5Y). Relatively few eagles were killed in winter, when wind speeds were lower and turbines were more often idle. Of the 52 turbine-killed eagles for which genetic material was sufficient for SNP sex identification, 23 were females and 29 were males.

For the 62 turbine-killed individuals for which DNA was sufficient for genotyping at 9 microsatellite loci, mean observed heterozygosity (H_O), expected heterozygosity (H_E), and allelic diversity were 0.50 (SE 0.06), 0.52 (0.07), and 4.6 (0.7), respectively (Supporting Information). For the 52 turbine-killed individuals for which DNA was sufficient for genotyping at 159 SNPs, mean H_O and H_E were both 0.34 (SE 0.01) (Supporting Information). Likelihood values of K from STRUCTURE analyses of SNP data from APWRA-killed Golden Eagles were consistent with a single panmictic population (Fig. 1 & Supporting Information), but APWRA-killed eagles were genetically distinct from reference samples obtained from Golden Eagles in eastern North America (i.e., $K = 2$) (Supporting Information). Nuclear microsatellite data were consistent with those from the SNP analyses.

Three unique mtDNA haplotypes were identified in eagles killed at APWRA, 2 of which had a frequency of 0.20 (SE 0.06) and the third a frequency of 0.60 (0.07). There were moderate levels of haplotype ($h = 0.57$ [0.06]) and nucleotide ($\pi = 0.001$ [0.001]) diversity. An mtDNA analysis of molecular variance indicated local and nonlocal birds were genetically different ($\Phi PT = 0.15$, $P = 0.02$).

No feathers from our known-origin birds or the eagles killed at APWRA had both $\delta^{13}C$ values >-20‰ and $\delta^{15}N$ values >11‰ (Supporting Information). Thus, all the birds in our study ate primarily terrestrial prey and were therefore suitable for use of δ^2H values to infer their geographic region of molt. We observed a strong positive
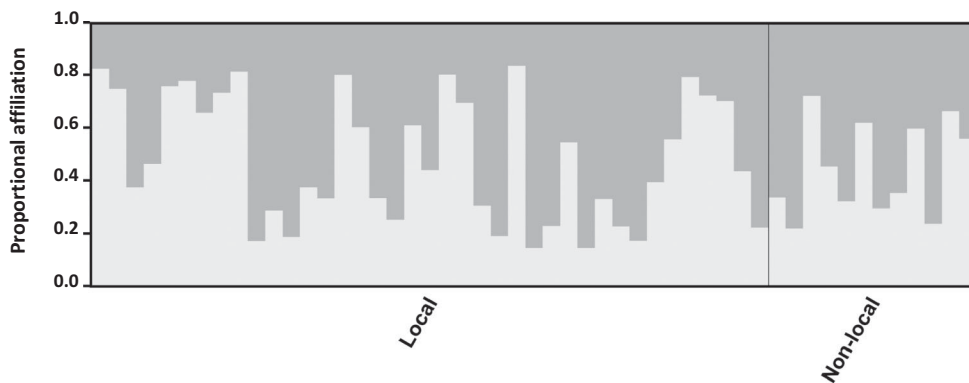
Figure 1. Results of STRUCTURE analysis for 52 Golden Eagles killed at Altamont Pass Wind Resource Area and genotyped at 159 single-nucleotide-polymorphism loci that considered K *values 1–5 (numbers of populations). Local and nonlocal designations were determined from stable isotope analyses. STRUCTURE results were CLUMPP-averaged across 10 runs when* K = 2 (assumed).
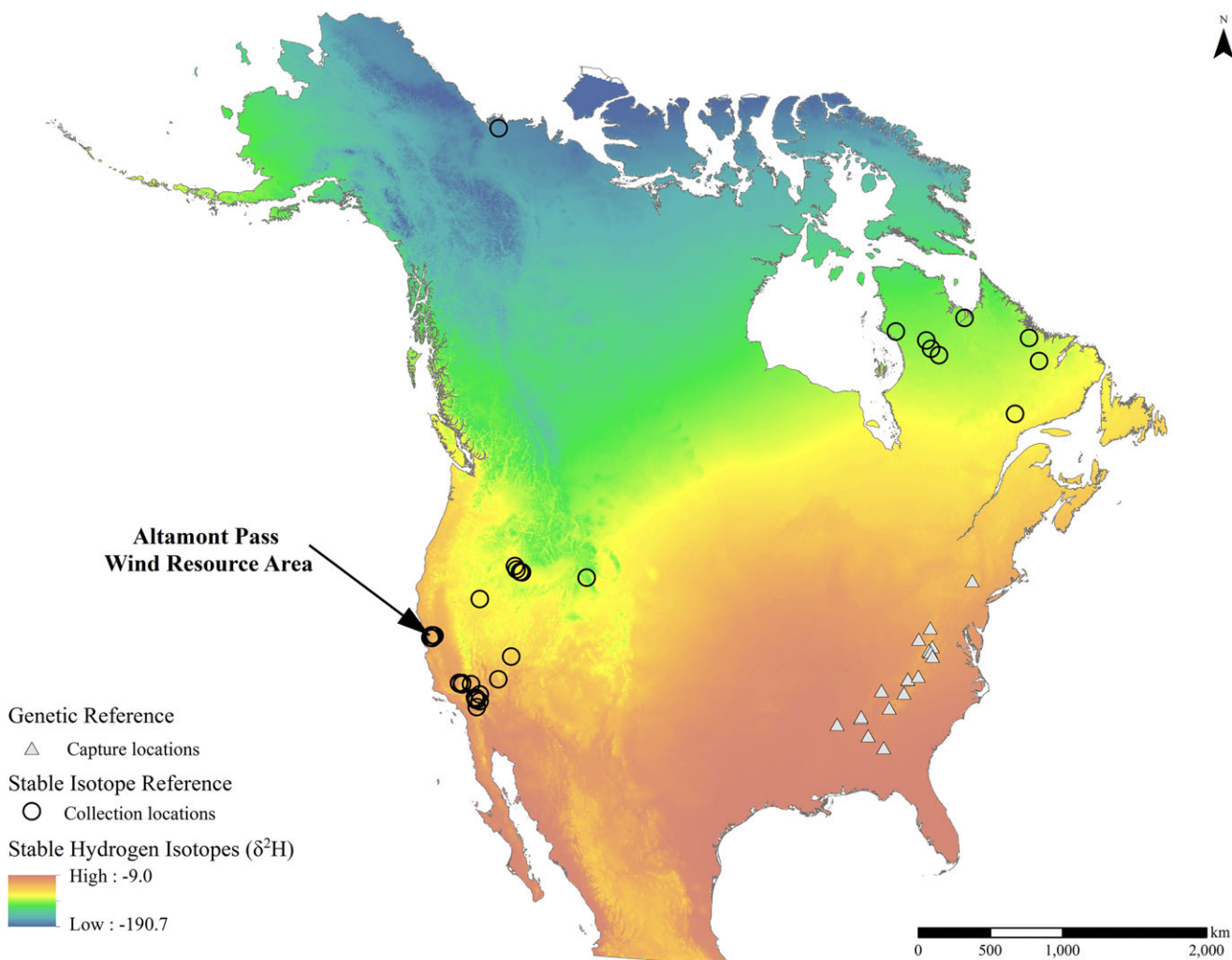

Figure 2. Map of predicted $\delta^2 H$ *values of May–August precipitation in North America (1980–2009) determined with IsoMAP (job 41700, available at www.isomap.org) that shows collection locations or summering grounds of the 44 Golden Eagles used to validate the stable-isotope approach for geographic assignment and the capture locations of the 27 Golden Eagles from eastern North America that were used as reference samples in genetic analyses.*

relationship between mean δ^2H_f values and May–August δ^2H_p values ($r^2 = 0.87$).

The isopleth classification data for the 44 Golden Eagles of known origins were best fit with a log-normal distribution (Supporting Information). When we evaluated expected accuracy assignment for eagles of unknown origin across all possible relative probability intervals the expected accuracy remained high and nearly constant across a range of probability intervals up to about 0.75. Probability intervals (Supporting Information) were equal to 1 minus the minimum isopleth values (Supporting Information); therefore, these metrics of assignment accuracy increased in opposite directions but were equivalent at 0.5.

Our Monte Carlo method to determine probability of origin indicated that 26% (17 of 66) of the Golden Eagles killed at APWRA immigrated to the APWRA within about 12 months (the approximate replacement time for an eagle body feather) preceding death (i.e., they had Monte-Carlo derived average relative probability values of <0.5 [nonlocal]) (Fig. 3a & Supporting Information). The minimum distances between APWRA and the nearest boundary of a 0.5 isopleth for these nonlocal birds ranged from 0 to 837 km (median = 110 km, mean = 146 km) (Fig. 4). Actual distances these birds traveled to APWRA were likely far greater than those minima. However, it was difficult to constrain the absolute distance with δ^2H data alone because of the strong latitudinal but relatively weak longitudinal resolution of δ^2H_p values across North America (Fig. 2). Qualitative interpretation of likelihood-of-origin maps (Supporting Information) suggested that at least 4 of the nonlocal individuals (5628, 5866, 5894, and x12-062) originated from north or east of APWRA and that at least 6 (6018, 6237, 6265, 6271, v14-013, and x14-027) originated south of APWRA; the origins of the remainder were ambiguous.

Probability of nonlocal origin was not influenced by the age of the bird ($\chi^2 = 3.38$, $p = 0.18$, df = 2) (Fig. 3b), month in which the eagle carcass was found ($\chi^2 = 10.29$, $p = 0.41$, df = 10) (Fig. 3c) or by sex ($\chi^2 = 0.49$, $p = 0.48$, df = 1) (Fig. 3d). However, a greater proportion of the youngest birds (HY-2Y) killed grew feathers far away from the APWRA (35% nonlocal) than subadults (3Y-4Y 11% nonlocal) and adults (≥5Y 19% nonlocal). The proportion of turbine fatalities composed of nonlocal birds was highest (50%) in August and the lowest (0%) in July, September, November, and January (Fig. 3c).

The 1144 Golden Eagle banding and recovery records spanned 87 years (1926–2013) and provided insight into the extent of Golden Eagle movements in North America. Of these recoveries, 350 were recorded at least once within 500 km of the APWRA. The average (SD) distance moved between banding and recovery of those 350 birds was 133 (257) km. The majority of birds (329 of 350) were encountered within 500 km of where they were banded (range 0–1488 km). Twenty-one of those 350 records had either a banding or recovery event >500 km distant from APWRA. Most birds (81%; 284 of 350 records) were both banded and recovered within California (Supporting Information). The states with the second and third most frequent number of records were Nevada and Oregon; no other state had more than 4 records.

Demographic models that did not incorporate immigration showed that about 11% of Golden Eagles at the APWRA should be 2Y individuals (Hunt 2002). However, the age structure of the eagles killed at APWRA was heavily skewed toward young birds (Fig. 3b). Based on previously published survival rates, it was not possible to replicate with models the age structure of the eagles killed. After incorporating immigration rates of 1.4 2Y and 0.8 3Y eagles per nest in APWRA, the age structure from the model came close to matching that of killed eagles (Supporting Information). In this modeled scenario, 28% of the population in any given year was comprised of individuals that immigrated (nearly identical to the 26% immigration rate estimated from the stable isotope analysis). This suggests that the Golden Eagles killed at APWRA included a substantial proportion of immigrants and that preadults (2Y especially, but also 3Y and 4Y birds) were killed with greater frequency relative to adults than would be expected based on their estimated numbers. In conjunction with the stable isotope and genetic data we used, our models therefore suggested that, immigration, likely of 2Y–4Y birds who could then join the local nesting population, underpins the current apparent stability of Golden Eagle numbers in the region.

Discussion

We found that the demographic effects to Golden Eagles of wind-turbine-associated fatalities at the APWRA extended across a large portion of North America. Furthermore, because eagles are top predators, such changes to their demography can have ecosystem-wide impacts. Our findings have relevance to understanding of the biology of Golden Eagle populations, to national and global conservation for this species, and to effective continental-scale management of recently mandated wind-energy development.

Implications for the Biology and Conservation of Golden Eagles

In North America, eagles are protected by the U.S. Bald and Golden Eagle Protection Act, the Migratory Bird Treaty Act, and numerous state, provincial, and national regulations (USFWS 2013; Guerra-Paramo et al. 2015). Nevertheless, eagles are regularly killed at wind-energy facilities (Pagel et al. 2013), and recent permitting regulations are designed to allow some sustainable take
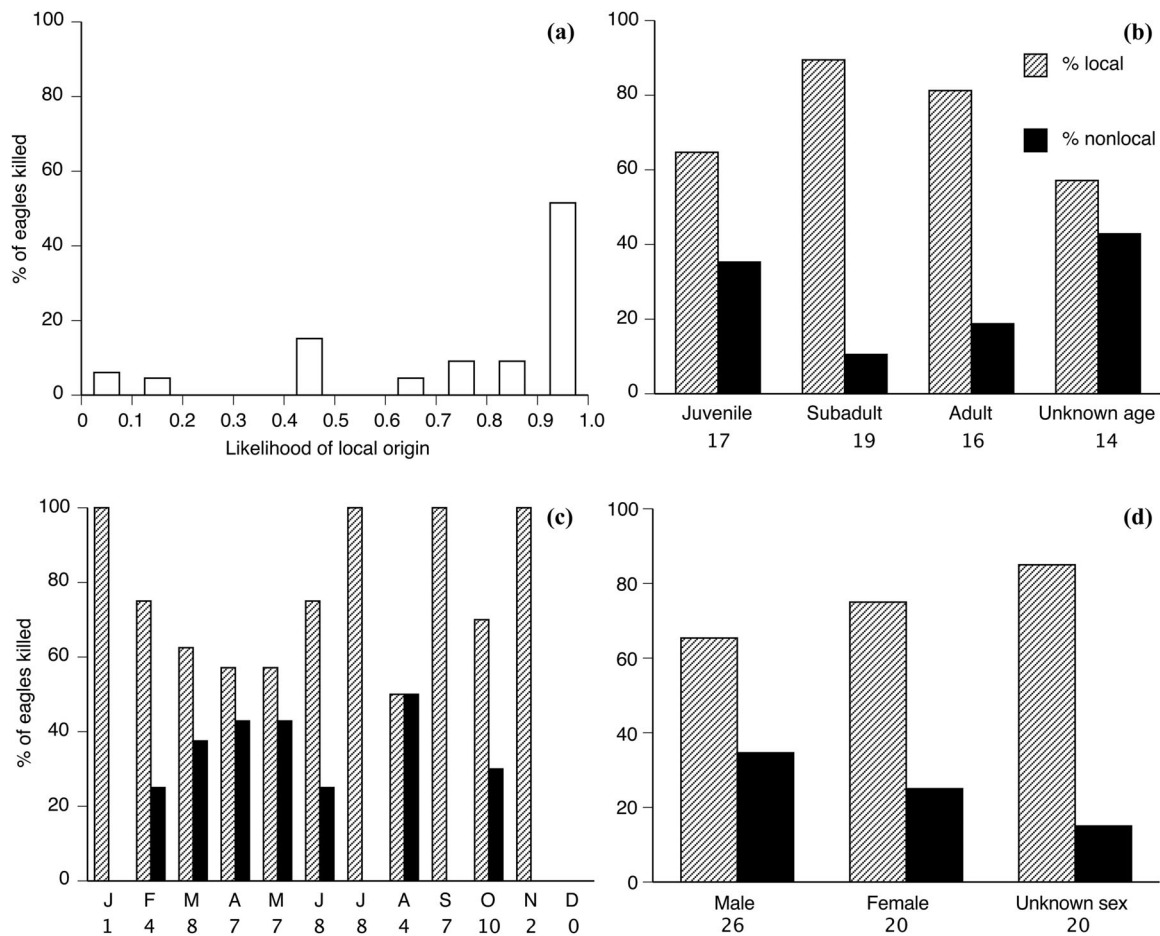
Figure 3. Origin and age structure of 66 Golden Eagles killed at the Altamont Pass Wind Resource Area (APWRA), California: (a) probability of origin of Golden Eagles killed at APWRA (>0.5, local; <0.5 nonlocal); (b) percentage of local versus nonlocal Golden Eagles by age; (c) percentage of local versus nonlocal Golden Eagles by month carcass was found; and (d) percentage of local versus nonlocal Golden Eagles by sex (numbers below x-axis labels, number of samples per age, month, or sex, respectively; HY–2Y, juvenile; 3Y–4Y, subadults; ≥5Y, adults).

of eagles, especially for renewable energy production (USFWS 2009). Previously, the geographic scope and demographic consequences of this take had not been explored empirically.

Our finding that the APWRA is an ecological sink provides important perspectives on management of North American Golden Eagle populations. The approximately 25% of birds originating from outside the region likely come to the site because it provides 2 main resources that pre-adult Golden Eagles require—food and updrafts to subsidize flight. However, a second-year bird that immigrated to the APWRA and was killed there 24 months later would have molted its body feathers in Altamont prior to its death and thus, in our analyses, would be considered local. As such, the proportion of nonlocal individuals in the population almost certainly is greater than the approximately 25% we observed.

With a stable regional population of about 75 nesting pairs (Hunt 2002) (more recent larger estimates in

Wiens et al. [2015] are for a larger geographic area), our modeling results suggest this population should be composed of about 150 breeding adults, 30 nonbreeding (floating) adults, and another 100–150 preadults, or a total of about 330 eagles. An eagle population of this size should have preadult mortality of about 25%/year (25–40 individuals/year) and adult mortality of approximately ≤10%/year (15/year) (Katzner et al. 2006). An estimated 28–68 Golden Eagles are killed each year at APWRA (Smallwood & Thelander 2008; ICF International 2014). Thus, if turbine-induced mortality is compensatory, then there is limited room for other forms of mortality. In response to concerns about this eagle mortality, recent replacement of old turbines at the APWRA was informed by scientific studies and appears to be reducing mortality rates (ICF International 2014). However, California Golden Eagles are exposed to and die from a number of other threats, especially lead poisoning, electrocution (Kochert & Steenhof 2002), and more recently drought.
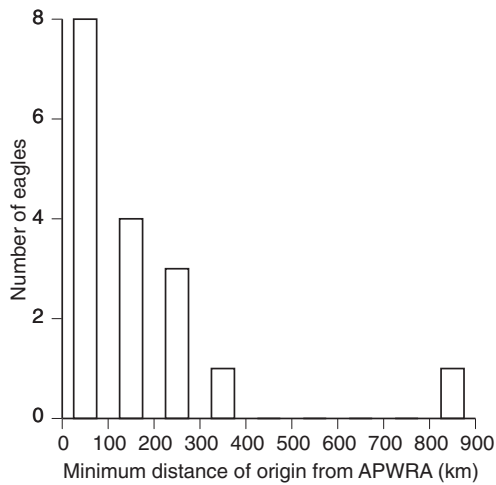
Figure 4. Minimum distance of travel (minimum distance from the APWRA to the nearest boundary of a 0.5 isopleth) by nonlocal Golden Eagles killed at the Altamont Pass Wind Resource Area (APWRA), California. Isopleths describe the likely origin of each bird, interpreted from δ²H values of feathers and of modeled May–August precipitation.

Therefore, our data suggest that for these eagles, turbine-associated mortality is additive and that the local eagle populations appear stable only because of sustained immigration from elsewhere in North America.

Accounting for additive mortality in demographic models and management plans involves accurately identifying the geographic extent of the focal population being modeled and managed. Our stable isotope and genetic data suggest the Golden Eagles killed at APWRA are drawn from much of the species' North American distributional range west of the Mississippi River. Multi-locus nuclear SNP (and microsatellite) data identified no genetic differentiation between local and nonlocal birds. There was some indication of genetic differentiation with the single mtDNA locus, but more data are needed to determine the relevance of these patterns, given the idiosyncrasies of mtDNA (Fahey et al. 2014). Together with telemetry (McIntyre et al. 2008; Braham et al. 2015) and banding data, the isotope and genetic data imply that California, Nevada, Idaho, Colorado, Arizona, New Mexico, Wyoming, and Oregon are the most likely sources of these eagles. Those states support large populations of nesting Golden Eagles, and, at certain times of the year, large numbers of migrant eagles from breeding populations in Canada, Alaska, and the American southwest.

The U.S. Fish and Wildlife Service has identified a management goal of no net loss to the size of Golden Eagle populations in the western United States (USFWS 2013). This goal is predicated on the demographic stability of eagle populations (Millsap et al. 2013). Our results show that Golden Eagle fatalities at one site have demographic consequence to a structured population that extends across much of the species continental range. This has at least 3 significant implications. First, the distribution and magnitude of eagle fatalities from all sources (electrocution, poisoning, collision, etc.) may explain why populations of Golden Eagles in western North America are not increasing from the previous lows of the middle of the twentieth century, as are many other raptor populations (Farmer et al. 2008; Millsap et al. 2013). Second, management of potential threats to Golden Eagles likely will be most effective if it considers cumulative mortality effects at a spatial scale not previously evaluated. Third, if existing genetic structure is taken into account, mitigation of turbine-associated mortality could occur in other parts of the western United States and have localized benefits for this interconnected population.

Implications For Renewable Energy Development

Contextualizing the mortality of these eagles has important implications for understanding of the continental-scale population dynamics of many species of wildlife killed at wind-energy facilities in the United States (e.g., Hayes 2013; Loss et al. 2013; Pagel et al. 2013) and globally (e.g., Desholm & Kahlert 2005; Drewitt & Langston 2006; Dahl et al. 2005). This is especially the case for long-lived species. Like eagles, bats are k selected (i.e., the stability of their populations depends on low adult mortality), and they may be killed in large numbers at wind-energy facilities. Likewise, there is concern among developers and managers that geese, sea ducks, and other similar taxa may also experience negative consequences from turbines (although some avoid wind facilities [Desholm & Kahlert 2005; Plonczkier & Simms 2013]). Although it is known that certain species killed at a wind facility may be from a large geographic area (Lehnert et al. 2014; Pylant et al. 2016), no previous studies link the spatial scale of renewable energy-associated fatalities to their actual demographic consequences. Our results with Golden Eagles imply that these other species may be well served by evaluation of local demography and of the potential continental-scale impacts of fatalities they encounter.

Effective management of energy production is improved by an understanding of its consequences, locally, nationally, and globally. The benefits of renewable energy production related to reduced greenhouse-gas emissions are important. However, energy producers, energy consumers, and government regulators have an interest in making renewable energy as environmentally sustainable as possible. As such, it is important to the continued growth of the renewable-energy industry to find mechanisms to minimize, mitigate, and reduce negative consequences of energy extraction to ecosystems. Few preconstruction environmental impact assessments consider consequences beyond local populations and ecosystems. Our data suggest the relevance of

accounting for these large-scale consequences in sustainable operation of renewable energy facilities.

Supporting Information

Detailed information on the study area, sample collection, genetic and stable isotope sample preparation, lab techniques, and data analysis (Appendix S1); the Leslie matrix model used (Appendix S2); data on microsatellite and SNP loci genotyped (Appendix S3, S4); stable isotope data (Appendix S5, S6); band recovery data by state (Appendix S7); stable age distribution of APWRA turbine killed eagles (Appendix S8); STRUCTURE analyses (Appendix S9, S10, S11); relational plots of δ^{13}C, δ^{15}N and δ^2H values (Appendix S12); best-fit probability density functions used to assign eagle origins (Appendix S13); expected accuracy of assignment for eagles of known origin across all possible relative probability intervals (Appendix S14); relationships between feather δ^{13}C and δ^{15}N values and frequencies of mean δ^2H values of May-August precipitation (Appendix S15); age-specific plots of δ^2H values of May-August precipitation for Golden Eagles killed at APWRA (Appendix S16); and likelihood of origin maps and 0.5 isopleth contour lines for Golden Eagles of known summering location, killed at APWRA and classified as nonlocal and killed at APWRA and classified as local (Appendix S17, S18, S19). The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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